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Nest site selection by Loggerhead Shrike (*Lanius ludovicianus*) in a fragmented landscape

Jennifer L. Froehly,^{1,3*} Amy K. Tegeler,² and David S. Jachowski¹

ABSTRACT—Understanding which factors influence nest site selection can lead to more effective species conservation. The Loggerhead Shrike (*Lanius ludovicianus*) has experienced severe declines since the 1940s and could potentially benefit from fine-scale management for nesting habitat, especially where fragmentation impedes conservation at the landscape scale. We examined how habitat characteristics at the nest tree and territory core scales influenced nest site selection by Loggerhead Shrikes in the coastal plain of South Carolina. We found 41 Loggerhead Shrike nests and measured habitat characteristics at the nest site and at available sites to model selection factors at the tree and territory core scales. Loggerhead Shrikes selected for low heterogeneity of vegetation density, high heterogeneity of vegetation height, and lower shrub and tree densities at the territory core scale. Loggerhead Shrikes also preferred nest trees with larger diameters at breast height. Overall, Loggerhead Shrikes appeared to select for nest site characteristics that enhanced foraging ease and success, and limited predation risk. We suggest that landowners in the southeastern coastal plain increase grassy habitat on their property and retain large trees in suitable nesting locations to increase optimal nesting habitat for Loggerhead Shrikes. Received 14 January 2019. Accepted 24 November 2019.

Key words: discrete choice, habitat selection, land use, *Lanius ludovicianus*, territory

Selección de sitios de anidación por el alcaudón *Lanius ludovicianus* en un paisaje fragmentado

RESUMEN (Spanish)—Entender qué factores influyen la selección de sitios de anidación puede determinar la conservación efectiva de las especies. El alcaudón *Lanius ludovicianus* ha experimentado declives severos desde la década de 1940 y podría ser potencial beneficiario de manejo a escala fina de su hábitat de anidación, especialmente donde la fragmentación impide la conservación a escala de paisaje. Examinamos cómo las características del hábitat alrededor del árbol del nido y en el núcleo de su territorio influenciaron la selección de sitios-nido de los alcaudones en la llanura costera de South Carolina. Con el propósito de modelar los factores de selección a escalas de árbol y núcleo de territorio, encontramos 41 nidos de alcaudón y medimos características del hábitat en sitios de anidación y en sitios disponibles para ello. Los alcaudones seleccionaron una baja heterogeneidad en la densidad de vegetación, alta heterogeneidad en la altura de vegetación, y baja densidad de arbustos y árboles a escala de núcleo de territorio. Los alcaudones también prefirieron anidar en árboles con mayores diámetros a la altura del pecho. En general, los alcaudones parecen seleccionar sitios de anidación con características que favorecen la facilidad y éxito de forrajeo, y que limitan el riesgo de depredación. Sugerimos que los propietarios de terrenos en esta llanura costera incrementen el hábitat herbáceo en sus propiedades y mantengan árboles grandes en sitios de anidación que sean utilizables para incrementar el hábitat óptimo para la anidación de los alcaudones.

Palabras clave: selección de hábitat selección discreta, territorio, uso del suelo

Multiple habitat scales affect a species' success or failure. While landscape-scale habitat conservation is often needed to increase regional occupancy (Ribic et al. 2009), fine-scale habitat factors that are needed for nesting are often not represented by measures assessed at landscape scales (Johnson 1980). Since an individual is only able to attempt to produce offspring if nesting habitat needs are met (Walters 1991), limited fine-scale nesting factors can contribute to a decline in population viability. For example, warm- and cool-season grass plantings enrolled in the Conserva-

tion Reserve Program in Missouri provided nesting sites and increased populations of Grasshopper Sparrows (*Ammodramus savannarum*), Eastern Meadowlarks (*Sturnella magna*), Field Sparrows (*Spizella pusilla*), and American Goldfinches (*Spinus tristis*) (McCoy et al. 1999). Even in sink populations (i.e., where population growth is negative) of Dickcissels (*Spiza americana*) and Red-winged Blackbirds (*Agelaius phoeniceus*), nesting efforts in these Conservation Reserve Program fields may reduce the severity of the sink by providing nesting habitat within areas where these species otherwise would not have nested, thereby increasing the number of individuals that have at least some chance of productivity (McCoy et al. 1999). Thus, considering fine-scale nesting requirements for avian species is of great importance.

Fine-scale management actions can also be easier to implement than actions at the landscape

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scale, especially when land ownership is complex and varied. For example, in urban areas where natural cavities are limiting, installation of nest boxes may provide increased nesting opportunities and subsequently increased population numbers of cavity-nesting species like the Eastern Bluebird (*Sialia sialis*; Newton 1994). Also, planting native tree and shrub species in residential yards can increase insect abundance, which in turn helps to support higher densities of insectivorous birds (Narango et al. 2017). Thus, fine-scale management actions can enhance conservation opportunities for avian populations in areas that have otherwise undergone rapid habitat degradation and fragmentation at the landscape scale.

The Loggerhead Shrike (*Lanius ludovicianus*), a mid-sized passerine of North America, is one grassland bird that may benefit from fine-scale management for nesting habitat. The Loggerhead Shrike has exhibited a range-wide decline of at least 74% since the 1940s (Cade and Woods 1997, Rosenberg et al. 2016) with the Atlantic coast experiencing one of the highest regional population declines (−89%; Rosenberg et al. 2016). Consequently, the Loggerhead Shrike is a species of conservation concern in many state wildlife action plans. Recent findings predicted that Loggerhead Shrikes in South Carolina were more likely to occur in areas with high pasture percentages within 1 km of the individual (Froehly et al. 2019), suggesting that high concentrations of pasture will be important for the conservation of the species. In addition to selecting relatively large open grassland habitats, Loggerhead Shrikes have been found to select for finer-scale factors such as the number of foraging perches (Bohall-Wood 1987, Yosef 1993, Yosef and Grubb 1994) and the availability of nest trees or shrubs to establish a nest site in the breeding season (Gawlik and Bildstein 1990, Michaels and Cully 1998, Chabot et al. 2001, Esely and Bollinger 2001), although selection of fine-scale habitat characteristics seems to vary regionally. Across their range, Loggerhead Shrikes occupy numerous ecosystems such as sage-steppe, prairie, desert scrub, pinyon-juniper woodlands, pastures, and pine savannas (Pruitt 2000), each of which offer a unique suite of fine-scale habitat characteristics. Thus, further information on how Loggerhead Shrikes select nesting habitat in the southeast coastal plain could guide specialized fine-scale management actions to

promote both occupancy and productivity in the southeastern United States.

The objective of this study was to examine how fine-scale habitat characteristics within the breeding territory influence nest site selection by Loggerhead Shrikes in the coastal plain of South Carolina. We examined habitat selection by Loggerhead Shrikes at both the territory and nest-tree scale to provide insight into critical resources required during the breeding season. At the territory scale, we evaluated support for the hypothesis that ground cover type and structure influenced prey diversity and density, and thus foraging efficiency by Loggerhead Shrikes in grassland systems (Rotenberry and Wiens 1980). We also hypothesized that tree and shrub structure influenced core territory selection through the balance of nest predator evasion and perch density factors (Gawlik and Bildstein 1990, Yosef 1994, Chabot et al. 2001, Walk et al. 2006). Finally, we hypothesized that human-modified habitat factors including perch availability and human disturbance could influence territory core selection (Yosef and Grubb 1994). At the nest-tree scale we evaluated support for the hypothesis that nest tree selection would be influenced by predation risk (Martin 1993), environmental exposure (Luukkonen 1987, Gawlik and Bildstein 1990), and structural preference (Chabot et al. 2001). Our study provides recommendations for land managers and individual landowners on how to enhance nesting habitat for Loggerhead Shrikes across the fragmented southeast coastal plain.

Methods

Study area

We conducted our study within the South Carolina Coastal Plain where Loggerhead Shrike occupancy is relatively high (see Froehly et al. 2019). The South Carolina Coastal Plain is composed of 51% forest, 12% crop, 4% pasture, 8% developed, and 24% other (Homer et al. 2015). Land in South Carolina is 90% privately owned (Vincent et al. 2017, South Carolina Department of Administration 2018), although private property sizes range from plantations of thousands of hectares to residential houses on only a few hectares of land. We selected 2 study areas totaling 368,086 ha in the coastal plain of South Carolina (Fig. 1). One study area was located in

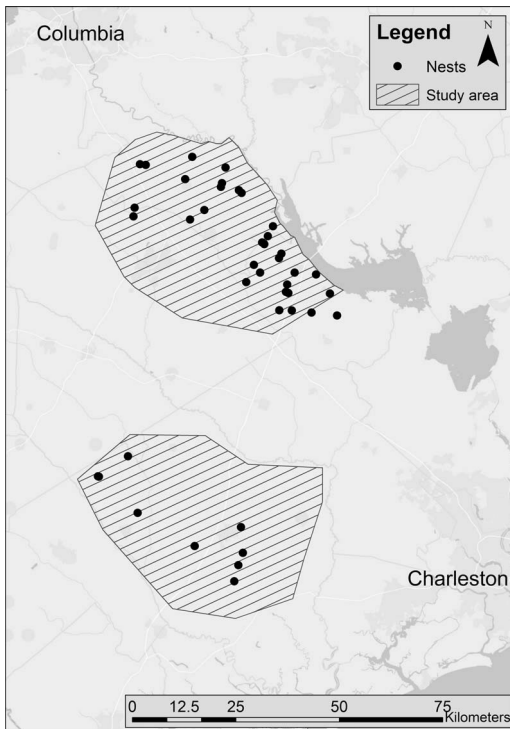


Figure 1. Location of study areas for Loggerhead Shrike point count surveys and nest searching in South Carolina, and location of nests from the 2016 and 2017 breeding seasons used in analysis.

Calhoun and Orangeburg counties, centered at Cameron, South Carolina, $33^{\circ}33'27''\text{N}$, $80^{\circ}42'55''\text{W}$. The other study area was located in Colleton County, centered at Walterboro, South Carolina, $32^{\circ}54'15''\text{N}$, $80^{\circ}39'58''\text{W}$. These study areas were chosen to maximize our ability to find shrike nests via detections from Froehly et al. (2019) and to represent a range of land cover conditions suitable for testing our fine-scale habitat selection hypotheses across the South Carolina Coastal Plain.

Data collection methods

In March–June 2016 and 2017 we used 3 techniques to locate Loggerhead Shrike nests within the South Carolina Coastal Plain. First, as part of a concurrent study (Froehly et al. 2019), we conducted unlimited radius point counts using a 10 min passive point count followed by a 6 min call playback period. We selected point count locations from roadside crop and pasture polygons using a

Generalized Random Tessellation Stratified (GRTS) sampling design in the *spsurvey* package (Kincaid and Olsen 2016) in Program R 3.3.3 (R Core Team 2017) so that survey points represented a range of sizes of crop and pasture polygons in our study area as defined by the National Land-cover Database (NLCD; Homer et al. 2015, see methods in Froehly et al. 2019). When a Loggerhead Shrike was observed during a survey, we remained after the survey to make extended visual observations to determine if the individual may be nesting and to locate the nest. Second, we made extended observations where there had been eBird sightings (particularly spring sightings) from the last 10 years, as Loggerhead Shrikes are known to reuse territories (Pruitt 2000). Lastly, we made extended observations at locations from expert sightings within the current field season, including sightings by state biologists and our own incidental sightings made while driving between point-count survey locations.

Once a Loggerhead Shrike was observed at a location, we obtained landowner permission to further search for and locate the nest. Nests were confirmed by visual observations of an individual building a nest, incubating eggs, or feeding chicks. After initially documenting nest locations, we minimized disturbance to the birds and controlled for potential confounding effects of variable vegetation growth by returning to the nest only during the last 2 weeks of our field season. At this point, if fledglings were present or the nest was abandoned, we measured habitat characteristics at both the territory core and nest tree scales. We defined the territory core as a 40 m radius circle centered on the nest tree, which is equal to the smallest reported Loggerhead Shrike territory size (Yosef and Grubb 1994) and within the distance extremes that other Loggerhead Shrike studies have used to analyze territory characteristics (2.5–100 m from the nest; Gawlik and Bildstein 1990, Chabot et al. 2001, St-Louis et al. 2010).

Within the territory core we counted the number of shrubs (woody stems <2 m in height), the number of trees (woody stems >2 m in height), and the number of artificial posts (Table 1). We measured ground cover vegetation structure in 2 transects radiating out from the nest tree at random directions using a modified “Wiens” pole method to quantify vegetation structure (Rotenberry and Wiens 1980, Michaels and Cully 1998). Specifi-

Table 1. Loggerhead Shrike tree scale and territory core scale (40 m radius) nest selection factors collected in South Carolina, USA, during the 2016 and 2017 breeding seasons that were used in a priori discrete choice models.

Variable	Description
Tree scale	
DBH	Diameter at breast height (cm)
l.branch	Distance from the ground to the lowest branch on the tree (m)
c.open	Average canopy opening percentage from densiometer readings at the trunk in each cardinal direction
Territory core scale	
H.Het	Maximum ground cover height heterogeneity. Coefficient of variation of maximum vegetation heights.
D.Het	Ground cover density heterogeneity. Coefficient of variation of vegetation total hits.
Grass	Probability of grass presence
Forb	Probability of forb presence
Litter	Probability of litter presence
Standing.dead	Probability of standing dead vegetation presence
Litter.depth	Average litter depth
dist.shrub	Distance to the nearest woody stem <2 m in height (m)
dist.tree	Distance to the nearest woody stem >2 m in height (m)
Shrubs	Number of woody stems <2 m in height within 40 m radius
Trees	Number of woody stems >2 m in height within 40 m radius
Posts	Number posts within 40 m radius
dist.post	Distance to the nearest post (m)
dist.powerline	Distance to the nearest powerline (m)
dist.building	Distance to the nearest building (m)
dist.road	Distance to the nearest road (m)
dist.crop	Distance to nearest row crop (m)

cally, we placed a 6 mm diameter rod vertically at 10, 20, 30, and 40 m from the nest tree trunk and recorded the number of times a piece of vegetation contacted the rod (separated by type: grass, forb, standing dead), height of the tallest live vegetation (cm), and litter presence and depth (cm). We used these ground cover data to calculate the probability of grass, forb, standing dead, and litter occurring at the territory core as well as vertical and horizontal heterogeneity (Table 1). We determined vertical heterogeneity by calculating the coefficient of variation of all the maximum live vegetation heights. Likewise, we determined horizontal heterogeneity by calculating the coefficient of variation of all the number of vegetation pole hits. Using a laser rangefinder, we also measured distance (in meters) from the nest tree to the nearest road, the nearest artificial perch, the nearest tree, the nearest shrub, the nearest powerline, the nearest building, and the nearest crop field (Table 1). These distances were not confined to the 40 m radius territory core.

At the nest tree we recorded tree species, nest height (m), the distance from the nest to the trunk

of the tree (m), height of the tree (m), height of the lowest branch (m), diameter at breast height in cm (DBH), and calculated the percent canopy openings from spherical convex densiometer readings at each cardinal direction taken with the observer's back against the trunk of the tree (Table 1).

To compare used nest sites to available nest sites, we also collected the same territory core and nest tree data on 2 nearby trees that were available for nesting. We chose nearby available trees by following a random compass bearing from the nest tree. We used the first woody structure (tree or shrub) encountered outside of 40 m as the unused available tree to ensure that we were sampling at least partially different territory core areas than the used territory core.

Analytical methods

We used a discrete choice modeling framework, where paired choice sets composed of one used nest site and two available nest sites were analyzed to provide the utility, or usefulness, of a location to an individual compared to the resources available to that individual (Cooper and Millsbaugh 1999).

We developed and evaluated support for 11 a priori models representing our hypotheses on territory core selection factors (Supplemental Table S1). These territory core models were subset into 3 groups of factors we hypothesized to influence ground cover type and structure, tree and shrub structure, and proximity to anthropogenic structures.

Four a priori models represented our hypothesis that ground cover type and structure influenced prey diversity and density, and thus foraging efficiency by Loggerhead Shrikes in grassland systems (Rotenberry and Wiens 1980). We predicted that the occurrence of grass, bare ground, forbs, and standing dead vegetation would increase selection while litter and litter depth would decrease selection by Loggerhead Shrikes (Rotenberry and Wiens 1980, DeGeus 1990, Gawlik and Bildstein 1990, Michaels and Cully 1998, Chabot et al. 2001). The influence of ground cover structure on Loggerhead Shrike habitat use has differed between studies, as studies occurring mainly in pasture report selection of short, uniform grass (Gawlik and Bildstein 1990), but studies occurring in more natural prairie landscapes report selection of high structural diversity (Rotenberry and Wiens 1980, Prescott and Collister 1993, Michaels and Cully 1998, St-Louis et al. 2010). Since there is little natural prairie habitat in South Carolina, we predicted that shrikes would select short, uniform ground vegetation structure.

Three a priori models represented our hypothesis that tree and shrub structure influenced core territory selection through the balance of nest predator evasion and perch density factors. In Ontario, isolated trees were more often selected as nest trees than non-isolated trees (Chabot et al. 2001), and areas with a higher density of trees (e.g., along fencerows) were associated with higher nest predation rates (including predation by small wild mammals, house cats, and snakes) in several populations of Loggerhead Shrike (Gawlik and Bildstein 1990, Yosef 1994, Walk et al. 2006). Thus, we predicted that low tree and shrub density and greater distances to the nearest tree and shrub would increase selection.

Four a priori models represented our hypothesis that human-modified habitat factors including perch availability and human disturbance could influence territory core selection. Shrikes are sit-and-wait predators and are known to benefit from a

high density of perches (Yosef and Grubb 1994); therefore, we predicted that low distance to powerline and nearest post, as well as post density, would increase selection. Shrikes also nest in fencerows along roads (Stewart 1975, Smith and Kruse 1992); therefore, we predicted that Loggerhead Shrikes would select for areas near roads due to the foraging opportunity that fencerows and mowed corridors commonly found along roadsides provide. Past research suggests that the influence of row crop agriculture on Loggerhead Shrike habitat selection may differ between populations, as Loggerhead Shrikes have been found to both use (Gawlik and Bildstein 1993) and avoid (DeGeus 1990) cropland. Since croplands do not offer any woody vegetation for nesting, we predicted that Loggerhead Shrikes would select for areas to nest away from cropland. Finally, we developed a global model and 6 sub-global a priori models to evaluate how multiple hypothesized factors influenced nest site selection at the territory core scale (Supplemental Table S1).

We developed 5 a priori models representing our hypotheses that nest tree selection would be influenced by predation risk (Martin 1993), environmental exposure (Luukkonen 1987, Gawlik and Bildstein 1990), and structural preference (Chabot et al 2001) (Supplemental Table S2). Specifically, we predicted that selection would occur for denser, larger trees with higher bottom branches because they offer more protection from predation and weather events like extreme rain or hail storms, and offer sturdy branches for nest building (Gawlik and Bildstein 1990).

We fit models in Program R using discrete choice modeling with the *mlogit* package (Croissant 2016). Prior to model fitting, we tested for correlations between covariates and did not include correlated covariates ($r > 0.65$) in the same model. In instances where correlated covariates occurred in the same model, we kept the most biologically plausible covariate. If correlated covariates were equally plausible we ran separate occupancy models with each singular covariate, and retained the covariate that produced the lower AIC_c score. We extracted the Log Likelihood from each model to calculate Akaike Information Criterion for small sample size (AIC_c) values and model weights (Burnham and Anderson 2002). We evaluated nest tree and territory core models separately and considered models within $2 \Delta AIC_c$

Table 2. Discrete choice model ranking for Loggerhead Shrike resource selection at the tree and territory core scales in South Carolina during 2016 and 2017. Models listed are those that contributed to the 90% cumulative model weight.

Model	K ^a	ΔAIC_c ^b	W_i ^c	Log L ^d
Territory Core Scale				
1. $\beta(\text{Shrub}) + \beta(\text{Trees})$ + $\beta(\text{D.Het}) + \beta(\text{H.Het})$	4	0.00 ^e	0.46	-32.73
2. $\beta(\text{Shrub}) + \beta(\text{Trees})$ + $\beta(\text{grass})$	3	1.93	0.18	-34.93
3. $\beta(\text{grass}) + \beta(\text{forb})$ + $\beta(\text{D.Het}) + \beta(\text{H.Het})$	4	2.69	0.12	-34.08
4. $\beta(\text{Shrub}) + \beta(\text{Trees})$	2	2.98	0.10	-34.55
5. $\beta(\text{Shrub}) + \beta(\text{Trees})$ + $\beta(\text{grass}) + \beta(\text{posts})$	4	3.64	0.07	-36.84
Tree Scale				
1. DBH	1	0.00 ^f	0.63	-40.13
2. DBH+c.open	2	1.54	0.39	-39.79

^a K = the number parameters in the model.

^b ΔAIC_c = the change in Akaike Information Criterion value corrected for small sample sizes from the top model.

^c W_i = the Akaike weight.

^d Log L = log likelihood of the model.

^e Territory core scale lowest AIC_c value was 68.79.

^f Tree scale lowest AIC_c value was 82.29.

units of the highest ranked model to influence selection, and further investigated effects of covariates within these models.

We validated each scale's top model(s) using k-fold cross validation (Boyce et al. 2002) if the Akaike weight was >0.25 . For each of 5 validation replications we randomly separated data so that 75% of choice sets (the nest and the 2 paired available points) made up the training dataset, and the remaining 25% of the choice sets made up the testing dataset. We ran the top models with the training data and used the resulting fitted models to calculate the relative probability of selection within each choice set. In each choice set, the model predicted correctly if the relative probability of the used site was higher than the relative probabilities of the available sites. We determined final model accuracy as the percentage of correctly predicted choice sets out of the 5 testing datasets.

Results

We located 15 nests between 4 April and 26 May 2016 and 26 nests (on different territories than in 2016) between 17 March and 31 May 2017, and collected habitat measurements on these

Table 3. Top model parameter estimates, standard error (SE), and 95% confidence intervals on Loggerhead Shrikes' relative selection probability at the territory core and tree scales in South Carolina during 2016 and 2017.

Covariate	Estimate	SE	95% CI
Territory core Model 1			
Shrub	-0.692	0.469	-1.630, 0.246
Trees	-0.657	0.434	-1.524, 0.211
cov.hits	0.892	0.496	-0.100, 1.884
cov.max.h	-1.085	0.545	-2.175, 0.004
Territory core Model 2			
Shrub	-0.798	0.466	-1.730, 0.134
Trees	-0.497	0.419	-1.335, 0.341
Grass	0.482	0.346	-0.210, 1.174
Tree Model 1			
DBH	0.625	0.243	0.140, 1.110
Tree Model 2			
DBH	0.589	0.253	0.083, 1.094
canopy.opening	0.157	0.221	-0.284, 0.598

nests and their paired points between 5 June and 18 June 2016 and between 21 May and 5 June 2017. Nests were mostly located within the primary study area boundaries, although 2 nests were located just southeast of the northern study area (Fig. 1). All nests were located on private property with the exception of 2 nests that occurred in a town park and at a county recycling facility. We found 10 nests in loblolly pine (*Pinus taeda*), 9 in live oak (*Quercus virginiana*), 4 in water oak (*Quercus nigra*), 3 in laurel oak (*Quercus laurifolia*), 2 in each of longleaf pine (*Pinus palustris*), black cherry (*Prunus serotina*), and sweetgum (*Liquidambar styraciflua*), and 1 nest in each of 9 additional tree, shrub, or vine species. Nests were located on average 6.9 ± 4.9 (SE) m above the ground and 3.8 ± 2.8 m away from the main trunk of the tree or bush.

Loggerhead Shrike habitat selection at the territory core scale was best explained by 2 top models (Table 2). The first top model included covariates of shrub and tree density, vegetation density heterogeneity, and vegetation height heterogeneity, and held 46% of the model weight (Table 2). Based on this top model, vegetation height heterogeneity and vegetation density heterogeneity most influenced probability of selection as these variables had the largest effect sizes and their confidence intervals barely overlapped zero (Table 3). Vegetation height heterogeneity had a positive effect on relative selection probability,

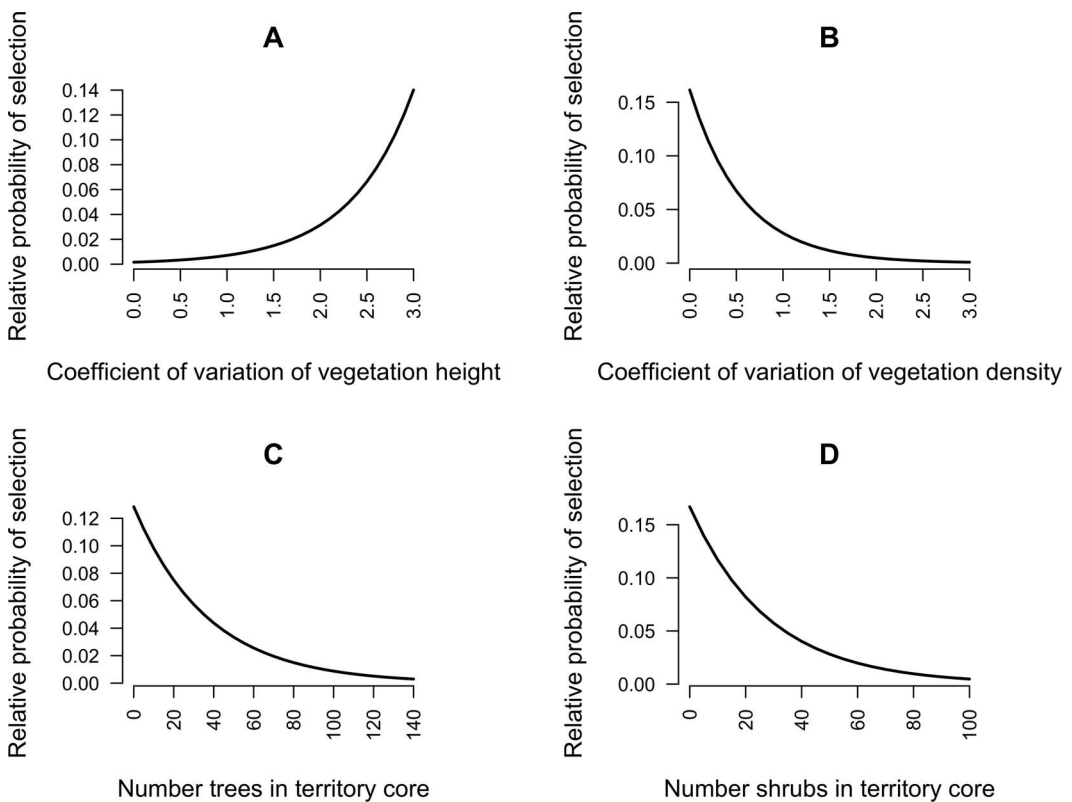


Figure 2. Influence of ground vegetation height variability (A), territory core ground vegetation density variability (B), tree density (C), and shrub density (D), on the relative probability of selection at the territory core scale by Loggerhead Shrikes in South Carolina during 2016 and 2017.

where predicted selection probability increased from 0.0 to 14% as variation increased from 1 to 3 (Fig. 2A). In contrast, vegetation density heterogeneity had a negative effect; as variation increased from 0.0 to 2.0, selection probability decreased from 16% to 0.0% (Fig. 2B). Both shrub and tree density had a slight negative effect on selection probability although their confidence intervals overlapped zero (Table 3, Fig. 2C and 2D). Cross validation resulted in a 43% chance that the model would correctly predict the used territory. The second top model had a similar slight negative effect of tree and shrub density on selection probability although their confidence intervals overlapped zero (Table 3). This model also included a slight positive effect of grass presence although confidence intervals overlapped zero (Table 2). These models supported our combined hypotheses that ground cover type and structure and that tree and shrub structure

influenced core territory selection, but did not support our hypothesis that human-modified characteristics influence territory core selection. The second ranked model was not cross validated as its Akaike weight was <0.25 .

Loggerhead Shrike habitat selection at the tree scale was best explained by 2 top models (Table 2). The first nest tree model included only DBH as a covariate and held 63% of the model weight, while the second ranked model included DBH and canopy openings and held 29% of the model weight, although canopy openings had a standard error larger than the estimate and therefore were likely not influencing selection (Table 3). These models supported our combined hypotheses that nest tree selection would be influenced by predation risk and environmental exposure. Our hypothesis that nest tree selection would be influenced by structural characteristics was not supported. We found that DBH had a relatively

slight, positive influence on selection probability, where trees with a 100 cm DBH had a relative selection probability of 3% and our maximum measured DBH of 165 cm had a relative selection probability of 10% (Fig. 3). Cross validation resulted in a 40% chance that the first ranked model would correctly predict the used tree and a 32% chance that the second ranked model would predict correctly.

Discussion

Our findings suggest that, as in other avian species, nest site selection by the Loggerhead Shrike in South Carolina is driven by factors that are likely to enhance foraging efficiency and success and reduce predation risk. Selection of factors that reduce predation risk are consistent with nest selection by other grassland and passerine birds (Hoover 2003, Eggers et al. 2006, Pearson and Knapp 2016). Likewise, characteristics affecting foraging success are important in many grassland and farmland birds as fragmentation and pesticide use in agricultural areas diminish insect and prey populations (Inselman et al. 2015, Stanton et al. 2016) and can directly affect the breeding pair (Yosef and Deyrup 1998). Indeed, shrikes in this region generally occupy areas with high pasture or grassland concentration within 1 km of their territory core (Froehly et al. 2019). Despite this sensitivity, however, Loggerhead Shrikes appear to be using nesting habitats that are characteristic of both natural and human-modified landscapes.

Similar to previous studies of Loggerhead Shrike nest selection in other portions of their range, ground vegetation structure was an important factor in territory core selection. Studies in South Carolina have noted that Loggerhead Shrikes nesting in pasture prefer short, uniform vegetation (Gawlik and Bildstein 1990), but Loggerhead Shrikes nesting in native prairie prefer higher diversity in vegetation structure (Rotenberry and Wiens 1980, Prescott and Collister 1993, Michaels and Cully 1998, St-Louis et al. 2010). Our prediction that Loggerhead Shrikes would select for nest sites in short, uniform ground vegetation structure was only partly supported, where individuals preferred to nest where territory cores contained low variation of ground vegetation

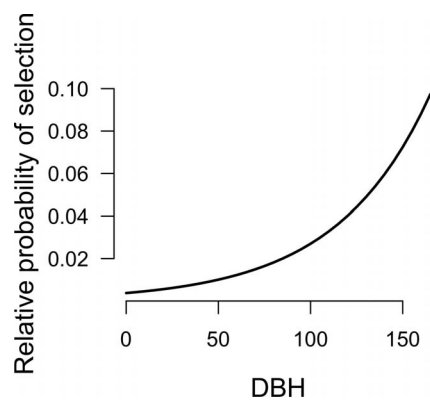


Figure 3. Influence of nest tree diameter at breast height (DBH) on the relative probability of selection at the tree scale by Loggerhead Shrikes in South Carolina during 2016 and 2017.

density but higher variation in vegetation heights. This result is likely a function of the habitat conditions specific to our study area. First, raw data from all used and available territories indicated that all ground cover was short (average maximum heights = 9.03 ± 8.77 cm) and sparse (average contacts = 1.48 ± 0.99). Therefore, it is likely Loggerhead Shrikes preferred consistently sparse ground vegetation that was also variable in height but typically not tall, which corroborates Yosef and Grubb (1993). Second, selection for nesting in areas with higher diversity of vegetation heights was likely a function of Loggerhead Shrikes selecting pasturelands for nesting rather than manicured lawns. Lastly, higher height diversity may be preferred by Loggerhead Shrikes because it likely has greater prey availability that could provide more prey items for foraging (Chabot et al. 2001, St-Louis et al. 2010). Additionally, Loggerhead Shrikes demonstrated some preference for territory cores with fewer shrubs and trees, likely to maximize the amount of grassy foraging area close to the nest and to minimize predation risk. To provide higher vegetation height diversity and improve foraging conditions in nesting territories for Loggerhead Shrikes, we suggest that residential landowners could delay lawn mowing, rotate mowing schedules, or establish a “meadow” section that is not mown.

In our study, Loggerhead Shrikes nested in a variety of tree species as well as in 2 vines on

fences and in one shrub, but overall selected trees with larger DBH measurements. Trees with larger DBH likely provide more and higher perches for detecting prey and potential nest predators (Bekoff et al. 1987, DeGeus 1990). Trees with larger DBH may be preferred by Loggerhead Shrikes because these trees could offer more defenses against snake predation since it is difficult for snakes to climb large trees (Rudolph et al. 1990). Further, given that Loggerhead Shrikes show high site fidelity and have been known to reoccupy previously used nest sites (Pruitt 2000), relatively old, large-diameter trees are likely important for shrikes returning to the same nesting territory year after year. In our study, a unique case of nest site fidelity was observed when one pair nested in a brush pile that contained their previous year's nest, even though there were other trees available in their territory. While a large DBH is not preferred in this example, it does demonstrate to what lengths a shrike will go to maintain a preferred nesting site. Our results suggest that landowners retain large trees in grassy habitat. Further, given evidence of high nest site fidelity, landowners should examine trees they are considering cutting down and conserve those that hold nests.

Our results reflect the habitat structure used by Loggerhead Shrikes while nesting, but our data do not address the relationship of habitat structure to reproductive success. Selection of nest sites is thought to be adaptive so that preferred sites offer high reproductive success (Martin 1998). However, sometimes seemingly ideal locations can act as ecological traps and decrease fitness (Dwernychuk and Boag 1972). For example, at the Savannah River Site, Indigo Buntings (*Passerina cyanea*) selected winged habitat patches that had 50% more edge than simple rectangular patches, but produced more fledglings from nests in the rectangular patches with less edge, possibly due to increased predation pressure in patches with more edge (Weldon and Haddad 2005). Several researchers have observed a high rate of car strikes with Loggerhead Shrikes near powerlines (Pruitt 2000), which could indicate an ecological trap. Therefore, it is essential for future work to determine how nesting success relates to selected nest sites. Additionally, we measured habitat variables after nests fledged or failed to reduce disturbance to the birds, though selection of a nest site occurs earlier, at nest initiation. This temporal

difference between selection and measuring habitat variables could potentially have led to a misrepresentation of some of our variables like grass height (Gibson et al. 2016). Thus, either measuring habitat at a more standard "nest hatch" date or examining how variables change through the breeding season will be important in future Loggerhead Shrike research to ensure that data is accurately portrayed.

Overall, while Loggerhead Shrike distribution and occupancy may be more strongly influenced by larger-scale habitat requirements like the amount of pasture and grassland in an area (Chabot et al. 2001, Froehly et al. 2019), or by the amount of forest (Johnson 2017), suitable nesting sites are still necessary for population recruitment. Ideally, both large and small scales should be managed so that all habitat requirements are met, but in areas with highly fragmented ownership, like in South Carolina, small-scale actions may be the only management option. Fine-scale nesting characteristics may be more easily managed within a single site, but can also have the ability to influence larger-scale factors through the cumulative effects of many landowners carrying out the same management actions (Jennings et al. 1999). Many landowners taking action to preserve specific habitat characteristics at small scales can help to increase natural habitat abundance and connectivity, and thereby decrease the severity of fragmentation and habitat loss at even the landscape scale (Marzluff and Ewing 2001). In order to promote nesting and to increase available habitat for Loggerhead Shrikes in the Southeast coastal plain, we recommend that private landowners maximize the amount of grassy habitat on their property, which will provide essential grassland habitat, retain large trees in open habitat to provide nesting substrate, and increase diversity in ground vegetation height to provide more high-quality foraging.

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